

KARYOTYPES IN RELATION TO CLASSIFICATION AND PHYLOGENY IN CLAYTONIA

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ABSTRACT

Chromosomal morphology in *Claytonia* involving symmetry, large size and few satellites is correlated with the gross morphologically less specialized species and their classification into sections, while karyotypes with asymmetrical and medium- or small-sized chromosomes having the most satellites typify the advanced perennials and one annual species studied. These data further suggest that there are at least two lines of evolution in the genus, viz. from sect. *Caudicosae* to sect. *Rhizomatosae* to sect. *Claytonia*, and from a taxon similar to *C. sibirica* to sect. *Limnia*.

In the classification of the genus *Claytonia* L. (*Portulacaceae*) proposed by Gray (1887) and as recently modified (Swanson, 1966; Nilsson, 1966), one annual and three perennial sections are recognized. Those species in the sect. *Caudicosae* with heavy taproots are considered primitive, those with rhizomes or runners in the sect. *Rhizomatosae* intermediate between the caudicose perennials and the specialized geophytic species of the sect. *Claytonia*, while the annual species of the sect. *Limnia* are also thought to be advanced. This subgeneric classification and proposed phylogeny are based only on morphological characters to which we now add data from chromosomal morphology.

Species of each section were studied: (1) *C. sibirica* L., sect. *Caudicosae*, $2n = 24$ (British Columbia: N of Squamish, Black Tusk recreational area, Lewis 6810, nr Sechelt, Sechelt Peninsula, Lewis 6827; Vancouver I, Cougar Creek at Hwy 19, Lewis 6822); (2) *C. cordifolia* S. Watson, sect. *Rhizomatosae*, $2n = 10$ (Washington: Kittitas Co, Table Mt Rd, Lewis 6736); (3) *C. sarmentosa* C. A. Meyer, sect. *Rhizomatosae*, $2n = 10$ and 15 from one population (Alaska: Hatcher Pass, Talkeetna Mts, Mitchell 927D1); (4) *C. virginica* L., sect. *Claytonia*, $2n = 12$ (North Carolina: Buncombe Co, 0.2 mi W of Swannanoa, Lewis 6582) and $2n = 14$ (Texas: Bowie Co, Texarkana, Suda 6); (5) *C. perfoliata* Donn ex Willd., sect. *Limnia*, $2n = 12$ (Washington: Kittitas Co, 10 mi W of Cle Elum, Lewis 6728).

Plants were grown in an underground room with 12 hr of light (500 ft candles) at 24°C and 12 hr of darkness at 18°C. Root tips excised from pot-bound plants were pretreated with low temperatures (0-2°C) for 16 hr and fixed by modified Carnoy's solution (4:3:1, chloroform-absolute ethanol-glacial acetic acid) for 30 min. After maceration in N HCl for 45 min, roots were immersed in 2% acetic-orcein for 24 hr. Temporary slides were made by the squash method; the best slides were then made permanent (McClintock, 1929) and are deposited in the Missouri

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Botanical Garden Herbarium (MO). Chromosomal measurements were made from photomicrographs enlarged 5600 $\times$; idiograms (Fig. 1-5) are based on arm ratios of chromosomes from 3-4 metaphase plates each from different root tips.

Chromosomal symmetry, length, number and satellite frequency for seven races of five species are summarized in Table 1. Certain trends are striking. For example, symmetry, expressed by pairs of V ($\pm$ median and symmetrical) and I (subterminal and asymmetrical) chromosomes and by percentages of subterminal chromosomes, is of three kinds. More or less symmetrical karyotypes are characteristic of *C. cordifolia* (Fig. 2) and *C. sarmentosa* (Fig. 3), those of *C. virginica* (Fig. 4-5) are strongly asymmetrical, while the karyotypes of *C. perfoliata* (Fig. 1) and *C. sibirica* are intermediate between these extremes. This grouping correlates at least in large part with the subgeneric classification, viz. species in the sect. *Rhizomatosae* differ markedly in chromosomal symmetry from *C. virginica* (sect. *Claytonia*), both of which differ from *C. perfoliata* of the sect. *Limnia*. The latter is similar to *C. sibirica* which is, however, an atypical member of the sect. *Caudicosae* forming a connecting link with the sect. *Limnia* (Swanson, 1966) a conclusion entirely confirmed by the degree of chromosomal symmetry.

On the basis of chromosomal lengths the five species separate into four groups corresponding exactly to their sectional classification (Table 1). Shortest chromosomes averaging 2.2 μ are found for the annual *C. perfoliata* (sect. *Limnia*), those of *C. sibirica* (sect. *Caudicosae*) are short to medium, those of *C. virginica* (sect. *Claytonia*) are still longer, while the longest chromosomes averaging 8 μ and 8.6 μ are found for *C. cordifolia* and *C. sarmentosa* (sect. *Rhizomatosae*), respectively. Since phylogeny and chromosomal size may be correlated with plants having larger chromosomes lacking evolutionary specialization (Davis & Heywood, 1963), the more primitive *C. cordifolia* and *C. sarmentosa* should possess large chromosomes. They do and, in fact, are the longest in the genus. The annual *C. perfoliata* with many specialized features (Swanson, 1966) has in contrast the smallest chromosomes; hence small chromosomes and evolutionary advancement are seemingly correlated as found for example in *Crepis* (Babcock et al., 1942). Chromosomes of the annual or perennial *C. sibirica* are also small and thus parallel *C. perfoliata* in this character as well as in symmetry and number. But only the tetraploid race

Table 1. Chromosome number, length, symmetry, and number of satellites per plate for *Claytonia* species.

	2n=	Length (μ)		Symmetry		Number of satellites
		range	average	pairs of V : I	per cent I	
<i>C. sibirica</i>	24	2.5-3.7	3.2	5:7	58	2
<i>C. cordifolia</i>	10	6.4-9.8	8.0	4:1	20	1
<i>C. sarmentosa</i>	10	7.5-9.8	8.6	5:0*	0*	1
<i>C. sarmentosa</i>	15	—	—	7.5:0*	0*	1
<i>C. virginica</i>	12	4.0-7.3	4.9	1:5	83	4
<i>C. virginica</i>	14	3.9-5.4	4.8	0:7	100	2
<i>C. perfoliata</i>	12	1.6-2.5	2.2	2:4	67	4

* one pair tending toward subterminal (I).

of *C. sibirica* was examined and as polyploids within a ploidy series generally have smaller chromosomes than diploids a direct comparison between this tetraploid and the other species studied (only diploid races) is not really possible. As noted the chromosomes of *C. virginica* are intermediate in size, yet a relationship with those of *C. cordifolia* and *C. sarmentosa* is indicated, i.e. structural alterations and loss in one arm of each chromosome of *C. cordifolia* (Fig. 2) or *C. sarmentosa* (Fig. 3) would give rise to smaller, asymmetrical chromosomes typical of *C. virginica* (Fig. 4-5).

We noted also that the number of satellites per karyotype varied by species and section (Table 1): maximum satellite frequency of species in the morphologically evolved sect. *Claytonia* and *Limnia* is 3.3 per mitotic plate, whereas those species in the more primitive sect. *Rhizomatosae* and the tetraploid *C. sibirica* average only 1.3 per plate. It appears that a multiplication of satellites is related to evolutionary advancement of chromosomes and of species *per se* quite apart from their level of ploidy.

Finally brief mention should be made of two infraspecific chromosomal differences illustrated by our results. *Claytonia sarmentosa* has been examined from only two localities in Alaska and already plants with $2n = 10, 14, 15, 16, 28$ and 32 are known. Further sampling will undoubtedly expand this impressive infraspecific aneuploidy and polyploidy and hopefully lead to an understanding of such divergence. These numerical differences, however, are not unique: *C. virginica* is known with no fewer than 45 races at many levels of ploidy and including extensive aneuploidy even at the diploid level (Lewis, 1967; Lewis et al., 1967a; Lewis et al., 1967b). A hint as to the origin of a diploid race is suggested by the $2n = 12$ cytotype (Fig. 4) which has a large median pair of chromosomes with secondary constrictions, a pair clearly absent from the $2n = 14$ race (Fig. 5). It would not be difficult to imagine breakage of the median pair at the centromere to form two $\pm$ similar pairs, such as those observed in the $2n = 14$ race, in which the (now) subterminally positioned secondary constrictions function as centromeres. Such an occurrence would give rise to a $2n = 14$ race from a presumed base of $x = 6$ for the species.

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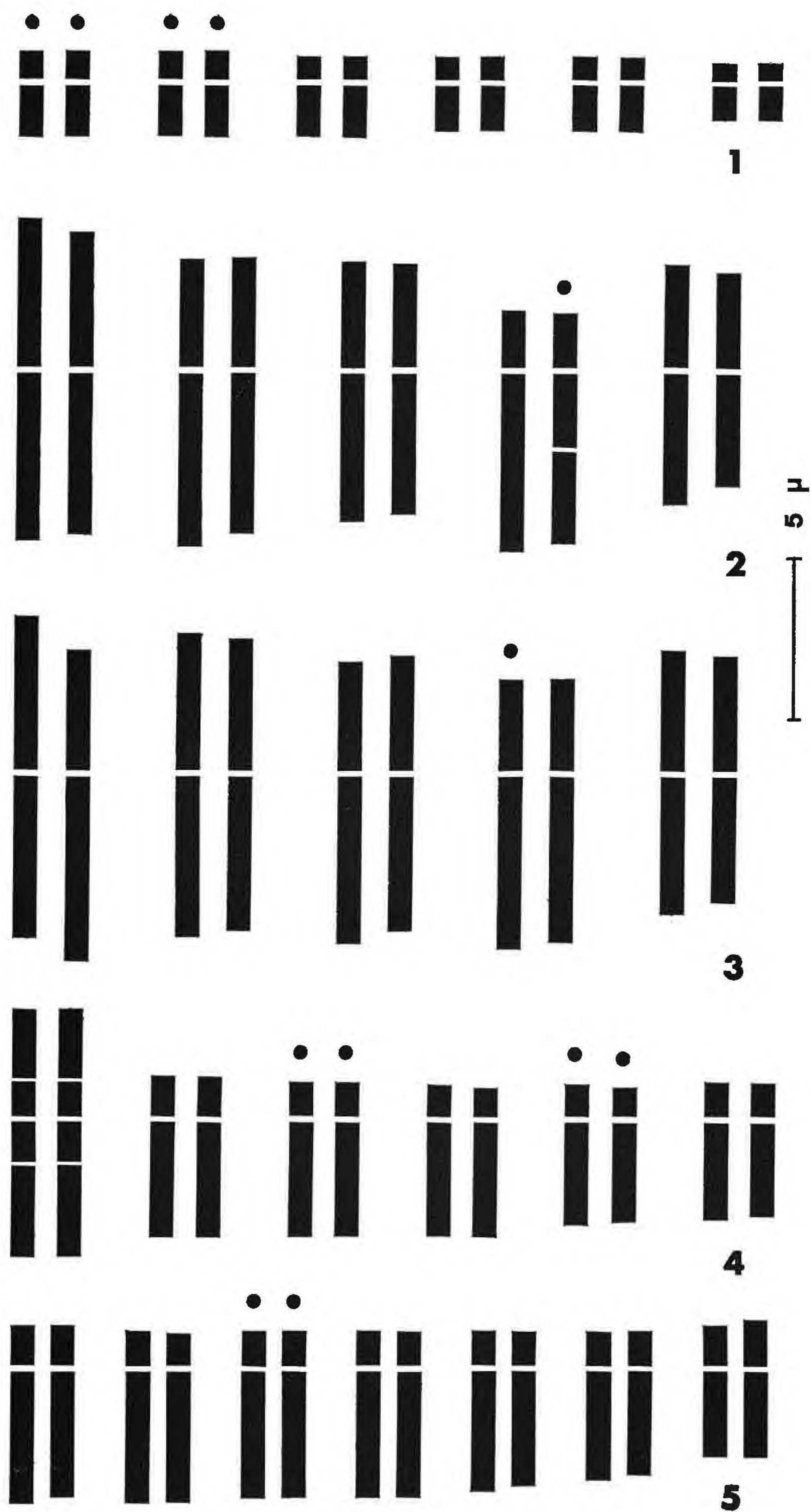


Fig. 1-5. Chromosomal idiograms of *Claytonia* species. Fig. 1. *C. perfoliata*, $2n = 12$ (Lewis 5728). Fig. 2. *C. cordifolia*, $2n = 10$ (Lewis 6736). Fig. 3. *C. sarmentosa*, $2n = 10$ (Mitchell 927D1). Fig. 4-5. *C. virginica*, $2n = 12$ (Lewis 6582), $2n = 14$ (Suda 6).